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Revision of the Myrmicine Genus
Acanthomyrmex (Hymenoptera: Formicidae)

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REVISION OF THE MYRMICINE GENUS *ACANTHOMYRMEX* (HYMENOPTERA: FORMICIDAE)

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ABSTRACT. The myrmicine genus *Acanthomyrmex* is revised in full. Eleven species of these dimorphic Asian ants are described, including six new species (*A. basispinosus*, *careoscrobis*, *concaus*, *foveolatus*, *laevis*, and *mindanao*). I distinguish two species groups, the *luciolae* group with six species and the *notabilis* group, with five. This informal division is supported by a cladistic analysis.

INTRODUCTION

Acanthomyrmex ants are endemic to Southeast Asia, including Sri Lanka (but as yet none have been recorded from India or New Guinea); the ants have very small colonies and are seldom collected (Moffett, 1985). I provide descriptions of the first new species of this genus to be recognized in a half century, and divide the species into two species groups. A cladistic analysis provides preliminary information regarding evolution within the genus.

All *Acanthomyrmex* species are dimorphic, with the genus including the most impressive examples of allometric growth known for the workers of ants. As an example, a major of *A. notabilis* selected from a Sulawesi series has a head length twice that of a minor worker from the same nest; because of differences in head shape, the cephalic volume is roughly ten times greater. Yet the major's antennae are only 5% longer than those of the same minor, while its trunk is only 3% longer, and roughly has a volume only 6% greater; furthermore, the body length of the

minor (trunk length + petiole length + postpetiole length + gaster length) is slightly larger than that of the major. The result is a major caste so absurdly proportioned that seen from certain angles live individuals appear to consist of little more than a head. Behavioral information on *Acanthomyrmex notabilis* and *A. ferox* (from the *notabilis* and *luciolae* species groups, respectively) indicates the majors serve roles in nest defense, and presumably also mill the seeds which apparently form a large part of the diet of these omnivores; in addition, majors occasionally participate in brood care (Moffett, 1985).

RELATIONSHIPS

The relationships between *Acanthomyrmex* species were studied using the program PAUP (version 2.3), written by David L. Swofford.

CHARACTER CODING FOR COMPUTER ANALYSIS

The characters and character state codes used in cladistic analysis are defined in the following section on terminology; the character states for each species and two possible outgroups are given in Table 1. The characters numbered 41 through 44 in Table 1 were of no value in determining species relationships and thus were excluded from the cladistic analysis. All characters were treated as binary or ordered. Polymorphism in a species (whether within or between series) was treated as if the data were missing for that species. Range limits for numerical characters

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TABLE 1. DATA MATRIX OF MORPHOLOGICAL CHARACTERISTICS FOR SPECIES OF *ACANTHOMYRMEX* AND TWO HYPOTHETICAL OUTGROUPS.†

Taxon	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
OUTGROUP																		
MYRMECININI	0-1	?	?	?	?	?	?	?	0	?	?	?	0	?	?	?	?	?
TETHEPA	1-2	?	0	?	?	?	?	?	1	?	?	?	?	?	?	1	?	0
LUCIOLAE GROUP																		
<i>A. basispinosus</i>	2	0	1	1	1	0	0	0	0	1	0	2	1	1	P	P	1	1
<i>A. crassispina</i>	1	0	P	0	0	0	1	1	2	P	1	1	0	0	0	0	0	1
<i>A. dusun</i>	?	0	?	?	0	0	?	0	?	1	1	1	?	1	1	?	?	?
<i>A. ferox</i>	0	0	0	1	P	1	P	0	0	1	0	0	0	1	0	0	0	0
<i>A. laevis</i>	0	?	0	?	?	?	1	?	0	?	?	?	?	0	?	0	0	0
<i>A. luciolae</i>	2	0	0	1	1	1	0	0	1	1	0	0	0	1	0	0	P	1
NOTABILIS GROUP																		
<i>A. careoscribis</i>	1	?	0	0	?	?	1	?	1	?	?	?	0	?	1	0	P	1
<i>A. concavus</i>	2	?	1	0	?	?	P	?	2	?	?	?	0	?	1	1	1	0
<i>A. foveolatus</i>	?	1	?	?	0	0	?	1	?	0	P	?	?	0	1	?	?	?
<i>A. mindanao</i>	1	1	1	0	0	0	1	0	1	0	1	2	0	1	1	1	0	P
<i>A. notabilis</i>	0	1	0	0	1	0	P	0	0-1	P	P	2	1	1	P	0	1	0

† In the table “?” refers to missing data and “P” refers to a polymorphic condition, or an intermediate condition, as discussed in the text. Character numbers refer to the characters that follow: 1. minor head shape; 2. major head shape; 3. minor greatest head width; 4. minor cephalic sculpture; 5. major foveate sculpture; 6. major rugose sculpture; 7. minor pilosity height; 8. major pilosity density; 9. CI (minors); 10. CI (majors); 11. cephalic hollow; 12. darkly pigmented medial streak; 13. frontal sulcus (minors); 14. frontal sulcus (majors); 15. clypeal index; 16. medial clypeal lobes; 17. lateral clypeal hairs; 18. clypeal rugae; 19. medial projection; 20. SI; 21. funicular index; 22. propodeal spine length; 23. pronotal spine length; 24. pronotal angle; 25. propodeal declivity; 26. propodeal spiracle diameter; 27. petiolar spines; 28. PWI; 29. subpetiolar declivity; 30. anterior petiolar peduncle length; 31. petiolar index; 32. lateral petiolar hair; 33. sublateral petiolar hair; 34. postpetiole narrowness; 35. postpetiole node; 36. postpetiole pilosity; 37. gaster pilosity; 38. femur concavity; 39. femur pilosity; 40. FLI; 41. FWI; 42. pronotal spine pilosity; 43. hypostomal teeth; 44. ventral mandible tooth.

were chosen to cleanly separate the maximum number of species; species were considered polymorphic when the values for a numerical character were spread on either side of these limits, or when the species was known from only the holotype and the value for that specimen was near to the limit. As more *Acanthomyrmex* material becomes available, it will become easier to evaluate characters for their usefulness in phylogenetic studies.

OUTGROUPS

The affinities of *Acanthomyrmex* are uncertain. Emery (1922) placed the genus in a subtribe of the Myrmecini along with *Pristomyrmex*, *Myrmecina* and *Dacryon*, because in these genera the lateral portions of the clypeus form only a

thin transverse ridge anterior to the antennal fossae (Fig. 1). In other myrmecine genera the clypeus is thicker and wider laterally. However, he was unable to provide any certain characters which uniquely define the Myrmecini as a whole. Kugler (1978) found that the morphology of the sting apparatus “does not support the unity of the Myrmecini,” while Wheeler and Wheeler (1954) found for larval characters that “each of the five genera studied might as well be in a different tribe,” and later found considerable differences between the larvae of *Acanthomyrmex ferox* and *A. notabilis* (Wheeler and Wheeler, 1977, 1983, and in preparation).

However, *Pristomyrmex* and *Myrmecina* show a number of apparent synapo-

bilis (Fig. 57). The strongly bulging eyes, the massive mandibles, and the small, well-separated mandibular teeth are possible synapomorphies. That *tethepa* is not a species of *Acanthomyrmex* is evidenced by a number of conspicuous characters, such as the elongate trunk, which has a very conspicuously impressed promesonotal suture, and the lack of a medial clypeal hair. Unfortunately, the major worker caste of this species is not known.

CHARACTER POLARITY

Although relationships among the outgroups are unclear, character states could be assigned for the ancestral conditions of *Acanthomyrmex* on the assumption that *Pristomyrmex* and *Myrmecina* are the two genera most closely related to *Acanthomyrmex*. If the state of a character was consistent within and between both these groups, the ancestral condition for *Acanthomyrmex* could unambiguously be assigned that state. If there was some variation in states, however, more distantly related genera had to be considered. For this purpose all of the additional genera which Emery (1922) placed in the tribe Myrmecini were treated as possibilities. When the state for that character did not vary within or between any of these genera (based on material available at the Museum of Comparative Zoology at Harvard), that state was assigned as the ancestral condition for *Acanthomyrmex* (unless either *Pristomyrmex* or *Myrmecina* showed the opposite state to that occurring in more distantly related groups, and it was impossible to assign a character state to the other of these two genera). For all other characters the ancestral state was given as uncertain.

This procedure is conservative in that before any ancestral state can be assigned as the ancestral condition of *Acanthomyrmex*, that ancestral condition must be supported by all possible outgroup trees. My assumptions are that *Myrmecina* and *Pristomyrmex* are the two groups most closely related to *Acanthomyrmex* and do

not in themselves form a clade, and that one or more of the other myrmecinine genera represent the next closest outgroups.

In a separate, very preliminary analysis, I discarded the hypothetical myrmecinine ancestral species and used the single species *Pheidole tethepa* as the outgroup for the genus *Acanthomyrmex*. Further studies on the phylogeny of *Pheidole* and allied genera will be required to evaluate whether *Acanthomyrmex* is in fact more closely related to *Pheidole* than *Pristomyrmex*, and, if so, to make possible a better resolved hypothetical outgroup for studies of *Acanthomyrmex* phylogeny.

CLADISTIC ANALYSIS

The entire data set was analyzed using the branch-and-bound method option of Swofford's PAUP program, which is based largely on the ideas of Hendy and Penny (1982). This method is guaranteed to find the shortest trees.

RESULTS

One of the five most parsimonious trees produced when a myrmecinine outgroup is used is given in Figure 2. The other, equally parsimonious trees differ from the first in having either *Acanthomyrmex dusun* or *A. careoscrobis* as the sister taxon to the remaining *Acanthomyrmex* species, or having *A. dusun* at the base of the *notabilis* species group clade, or *A. careoscrobis* at the base of the *luciolae* species group clade. Uncertainties in the placement of *A. dusun* and *A. careoscrobis* probably will be resolved upon collection of the minor worker caste of the former species, and the major worker caste of the latter.

These results suggest the possibility that both the *notabilis* and *luciolae* species groups are monophyletic (as in Fig. 2). The most significant character distinguishing these groups is the conspicuously emarginate posterior margin of the heads of major workers in species of the *luciolae* group (including *A. dusun*), versus the

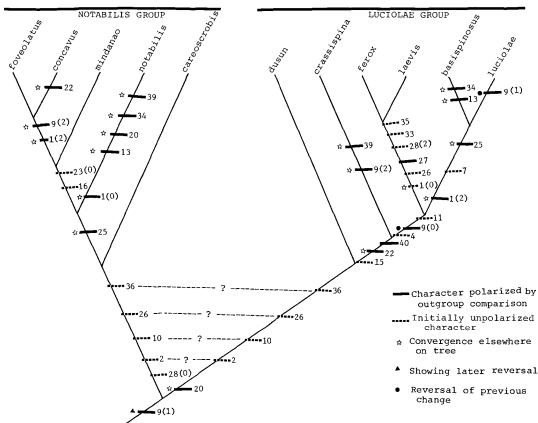


Figure 2. Proposed phylogeny of the genus *Acanthomyrmex*, given a hypothetical myrmecine outgroup. Four additional, equally parsimonious trees differ only in the position of the species *dusun* and *careoscribis*, as discussed in the text. All character state changes for initially polarized characters are mapped, but for simplicity only those unpolarized characters which show no homeoplasy within the *Acanthomyrmex* tree are shown. Numbers refer to characters as described in Table 1. Derived states are indicated in parentheses for multistate characters. Tree length: 78 steps.

more evenly rounded margin characteristic of majors in *notabilis* group species. The placement of the species in which the major caste has not yet been described (particularly *careoscribis* and *concavus*) should be considered tentative.

Two trees are most parsimonious when *Pheidole tethepa* is used as the outgroup. The first is identical to the tree shown in Figure 2, except it is rooted just below *ferox* and *laevis*, such that the *ferox-laevis* clade is the sister to all other *Acanthomyrmex*. Thus now the *luciolsae* species group is paraphyletic, with *A. dusun* representing the sister species to the *notabilis* group. The other tree is similar, but the

species *crassispina* is displaced so as to represent the sister group of all other *Acanthomyrmex*. In addition the *ferox-laevis* and *basispinosus-luciolsae* clades now form a monophyletic group. Given that *Acanthomyrmex* is related to *Pheidole*, both of these phylogenies would appear to be reasonable, since the emarginate head characteristic of *Pheidole* major workers is treated as the ancestral condition for *Acanthomyrmex*.

TERMINOLOGY AND CHARACTER STATES

All available *Acanthomyrmex* material was examined in detail for differences in

morphology before any attempt was made to distinguish species. The range of variation in those traits which showed appreciable differences between series was then apportioned into two or more discrete character states, regardless of whether the trait varied continuously or in a discrete manner. The resulting character state codes were then used in delineating species and for phylogenetic analysis.

The characters used in this revision are defined below (excluding characters for which one of two character states is unique to one species), along with the coding for each character state. Definitions of several commonly used terms are also given here. Sculpturing terminology follows that of Harris (1979). Measurements were made with an ocular micrometer on a Leitz microscope; all are significant to at least 0.01 mm. Indexes such as CI were calculated before converting micrometer units to millimeters. Scanning electron micrographs were prepared with a AMR 1000a SEM, using uncoated or gold-palladium coated specimens.

When not otherwise indicated, descriptions apply to both minors and majors.

CHARACTERS ON HEAD CAPSULE (EXCLUDING CLYPEUS)

Cephalic hollow (major workers). **Character states:** large, medial depression in vertex of head [0] either shallow and ill-defined or absent; or [1] prominent.

CI (Cephalic index). $100 \times \text{HW}/\text{HL}$. **Character 1, states** (minor workers): [0] at most 110; [1] intermediate; or [2] > 120. **Character 2, states** (major workers): [0] at most 95; or [1] > 95.

Darkly pigmented streak (major workers). Medial black line on head visible in dorsal full-face view [0] absent; [1] very short, only at back margin of head; or [2] longer, extending farther rostrad onto dorsal surface of head.

EL (Eye length). Diameter of eye in full-face view.

Frontal sulcus. **Character 1, states:** [0] mi-

nor workers without a short, wide sulcus conspicuous immediately above frontal area; or [1] sulcus present. **Character 2, states:** [0] major workers without a wide, deeply impressed sulcus between cephalic hollow and frontal area; or [1] sulcus present.

Full face. Head viewed dorsally so as to attain the maximum length.

Greatest head width. **Character states:** maximum HW is [0] about equal above and below eyes (difference 2% or less); or [1] greatest above the eyes.

Head shape (minor workers). **Character states:** in dorsal full-face view, back margin of head [0] rounded except for a very shallow medial concavity (e.g., Fig. 57); [1] moderately concave all the way across (Fig. 15); or [2] deeply concave, so that the posterior corners of the head are produced back into prominent, lateral lobes (Figs. 9, 44).

Head shape (major workers). **Character states:** in full-face view, back margin of head [0] distinctly bilobed (Fig. 11); or [1] evenly rounded, at most slightly emarginate medially (Fig. 48, 59).

HL (Head length). The maximum distance from the base of the medial hair on the clypeus to the medial point on the posterior margin of the head.

HW (Head width). The maximum width across the head in full-face view, excluding the eyes.

Hypostomal teeth (major workers; invariably present in minors). Small rounded projections, one located laterally near base of each mandible. **Character states:** teeth [0] absent; or [1] present.

Pilosity density. **Character states:** long erect to suberect hairs on head [0] numerous; or [1] very scattered.

Pilosity height. **Character states:** longest of the hairs on dorsum of head extending [0] < 0.10 mm; or [1] > 0.12 mm.

Sculpture (cephalic) (minor workers). **Character states:** dorsal and lateral surfaces of head capsule with [0]

rounded (or ellipsoidal) foveae having thick, curving walls; or [1] at least those foveae on vertex and adjacent to scrobes with angular borders, and separated by thin, lamellar walls.

Sculpture (cephalic) (major workers).

Character 1, states: foveae [0] relatively small; or [1] large. **Character 2, states:** frons [0] lacking costate sculpture; or [1] sculpture present.

CHARACTERS ON CLYPEUS, MANDIBLES AND ANTENNAE

Clypeal index. The shape of the region of the clypeus between the frontal carina was measured as $100 \times W/H$ where "W" is the minimum distance between the raised edges of the frontal carina, and "H" is the distance from the posteriormost point on the frontal area to the base of the medial clypeal hair. **Character states:** [0] at most 125; or [1] > 125.

Clypeal rugae (minor workers). Two longitudinal rugae extend through the clypeus from near the bases of the lateral clypeal hairs, delineating a medial clypeal region between them (e.g., Fig. 15). **Character states:** these rugae are [0] absent or incomplete; or [1] well-developed.

Funicular index. An index of funicular thickness: maximum width of funicular segments II and III (which are similar in shape) divided by the average length of the same segments (half the combined lengths of the segments). **Character states:** funiculi [0] thick, with index > 1.20 (or > 1.50 in majors); or [1] thinner.

Lateral hair on clypeus (minor workers). Long hair projecting forward at either side of medial hair from anterior margin of clypeus (Fig. 3). **Character states:** base of each lateral clypeal hair [0] not completely enclosed by a low wall; or [2] hair in a well-developed oval fovea (Fig. 3).

Medial hair on clypeus (minor workers). Hair projecting forward from ante-

rior margin of clypeus medially (Fig. 3).

Medial clypeal lobes (minor workers). A small, narrow projecting lobe located immediately to either side of medial clypeal hair, and mesad to the lateral clypeal hair (Fig. 3). **Character states:** lobes [0] feebly developed; or [1] strongly projecting.

Medial projection (major workers). **Character states:** [0] anterior margin of clypeus without a projecting medial lobe, although often with low, feebly rounded lobes (e.g., Fig. 17); or [1] projection present (Fig. 25).

MI (Mandible index). $100 \times ML/HL$.

ML (Mandible length). Distance between basal condyle and apical tooth of mandible.

SI (Scape index) (minor workers; little variation in majors). $100 \times SL/HW$. **Character states:** [0] at most 90; or [1] > 90.

SL (Scape length). The maximum length of the scape (excluding the wide flange at its base and the basal radicle beneath it).

Ventral mandibular tooth (minor workers). A tiny inward-projecting denticle present along the medioventral border of each mandible, where, in majors, a massive blunt projection is invariably present. **Character states:** denticle [0] absent, or [1] present.

CHARACTERS ON TRUNK AND LEGS

Femur concavity. **Character states:** ventral surface of each femur [0] convex or somewhat flattened; or [1] with a well-developed concave groove (at least in hind femora).

Femur pilosity. **Character states:** [0] each femur with at most two erect to sub-erect hairs visible in profile (in which case hairs typically present proximad on ventral face of shaft); or [1] hairier.

FLI (Femur length index). $100 \times HFL/HL$. **Character states:** index [0] at most

120 (or at most 60 in majors); or [1] greater.

FWI (Femur width index). $100 \times \text{HFW} / \text{HFL}$, where HFW is the maximum width of the hind femur in lateral view. **Character states:** [0] index at most 18; or [1] greater.

HFL (Hind femur length). Maximum length of the hind femur.

Pronotal angle. **Character states:** [0] anterior ventrolateral margin of pronotum curved to sharply angled, but without a small but distinct tooth (e.g., Fig. 16); or [1] tooth present (Fig. 24).

Pronotal spine length (minor workers).

Character states: [0] pronotal spines short and stubby, conspicuously shorter than propodeal spines (Fig. 52); [1] pronotal spines long, but not longer than propodeal spines; or [2] pronotal spines longer than propodeal spines (Fig. 24).

Pronotal spine pilosity. **Character states:** pronotal spines each with [0] at most two prominent erect to suberect hairs visible in profile; or [1] hairy (with more than two hairs).

Propodeal declivity. **Character states:** declivity of propodeum with [0] at most a single distinct rugum bordering each side, extending from the base of the propodeal spine; or [1] with two adjacent rugae along each border.

Propodeal spine length. Measured from the tip of the spine to the closest border of the propodeal spiracle. **Character states:** [0] propodeal spine less than half as long as length of head (HL) (or less than 25% of HL in majors); or [1] longer.

Propodeal spiracle diameter (major worker; little variation in minors).

Character states: [0] diameter of spiracle less than 2% of HL; or [1] spiracle opening larger.

CHARACTERS ON PETIOLE, POSTPETIOLE, AND GASTER

Anterior peduncle length, petiole. **Character states:** anterior peduncle rela-

tively short and deep (e.g., Fig. 43); or [1] peduncle long and more slender (e.g., Fig. 47).

Gaster pilosity. **Character states:** [0] gaster with numerous erect or suberect hairs (usually densest dorsad); or [1] gaster with very few hairs or bare.

Lateral petiolar hairs. **Character states:** [0] an erect hair extends laterally from each side of anterior petiolar node just caudad of the spiracle; or [1] hair lacking.

Petiolar index. $100 \times \text{PL} / \text{PH}$, where PL is the distance from the posterior margin of the petiolar spiracle to the dorsalmost point on the posterior margin of the posterior peduncle, with the petiole viewed in profile; while PH is the height of the posterior peduncle of the petiole. **Character states:** index [0] < 170; or [1] > 180.

Petiolar spines. **Character states:** petiolar node [0] lacking long spines laterally at apex although often with short lateral denticles (Fig. 8A-C); or [1] long spines present (Fig. 8D-F).

Postpetiole narrowness. **Character states:** [0] node relatively long, greater than 60% as long as it is wide in dorsal view; or [1] narrower.

Postpetiole node. **Character states:** [0] node high and rounded, sculpture lacking or foveate; or [1] node low, slightly convex or flattened, and rugose.

Postpetiole pilosity. **Character states:** dorsal face of postpetiole with [0] two pairs of hairs; or [1] pilosity different.

PWI (Petiolar spine width index). In dorsal view, distance between apical spines or denticles relative to the greatest width of petiole basally at node. **Character states:** tips of spines [0] close together (PWI < 65); [1] intermediate (PWI 65 to 100); or [2] projecting laterally (PWI > 100).

Sublateral petiolar hairs. **Character states:** [0] no erect hair extends ventrolaterally from each ventrolateral face of the anterior petiolar node at a posi-

sionally alveolate or virtually smooth. Eyes moderately large (length of eye in full-face view 17 to 25% of head length), oval, and strongly convex; located mediolaterally, with the distance between anterior margin of eye and mandible bases representing 24 to 34% of head length. Antennal fossae far apart, at anterior margin of head. Feeble scrobe usually present dorsad to eyes for all or at least the basal part of the scape (bent downwards apically in some species to accommodate part of the funiculus); the frontal carinae extend back to form the dorsalmost borders of the scrobes. Antennae 12-merous, moderately thick, with a three-segmented funicular club; club about as long as remainder of funiculus excluding basal funicular segment. There is a prominent flange above the basal radical, forming a thin, disk-shaped "base" to the scape.

Clypeus produced back between bases of antennae; posterolateral borders of clypeus raised to form trenchant ridges which border the antennal fossae in front. Clypeus usually with lateral foveae or rugae; anterior margin with several small, well-separated projecting lobes and with a prominent medial hair. Mandibles massive (MI 69 to 92), with a wide, subtriangular blade which curves ventrad toward apex, with the margin having four to ten tiny teeth separated by wide gaps in addition to two relatively prominent apical teeth; dorsal mandibular surfaces feebly punctate and with a very feeble rugulose microsculpture. Maxillary palpi with four segments; labial palps with three (*A. basipinosus* and *mindanao* examined).

Trunk very short and robust, evenly convex in profile, with anterior margin of propodeum not at all impressed dorsally; trunk diminishing in width posteriorly. Pronotum fused with mesonotum; promesonotal suture obsolete. Propodeum invariably bispinose; pronotum generally armed with dorsolateral spines, which are located anterodorsally to the dorsalmost point reached by the groove between the pronotum and mesothorax laterally.

Sculpture foveate on pronotum and dorsally on trunk; areolate-rugose on pleura of remainder of trunk, and smooth on declivity of propodeum. Petiole pedunculate in front; node usually with dorsolateral denticles or spines. Postpetiole variable, low and rounded dorsally or with a prominent node; usually rugose. Gaster oval, less wide than head, and longer than deep. Legs moderately long, with hind femora 85 to 148% as long as head; middle and hind tibiae with a single basal spur. Long, erect to suberect pilosity generally dense on head, sparser on trunk, and variable on legs, petiole, postpetiole and gaster; on head hairs mostly arise from foveae.

Major Worker. Head enormous, appearing greater in volume than remainder of body, and of a length about twice that of trunk or longer. Foramen located ventrally far from posterior margin of head, with the portion of the head behind the foramen extending back over the trunk; trunk partially hidden within a cavity beneath head posteriorly. Cephalic sculpture foveate (at least on vertex), but with foveae generally small, shallow and sparse relative to those of minor workers. Ocelli lacking; compound eyes similar to those of minor worker, but slightly more anterior on head, and of a length 9 to 14% of that of the head. Antennae similar in size to those of minor workers, and thus much smaller relative to head size; scrobes as described for minors but more prominent, with a shallow recess for basal portion of funiculus typically also present dorsad to eyes. Clypeus smooth, without small projecting lobes along anterior margin, and usually lacking pilosity. Mandibles massive, similar to minors but smaller relative to head size (MI ca. 50 to 60), typically with dorsal masticatory margin worn; with a ventral process shaped like a massive, blunt tooth beneath mandible basally (occasionally present as small denticle in minors). Trunk, waist, and gaster similar to minors, but pronotal spines lacking, and pronotum smooth anteriorly.

Queen. Previously undescribed. Head

(terminal segment about 80% of scape length). Mandibles as long relative to head length as in queen or major, but much less massive, only very slightly curved ventrad apically; the six to eight teeth along masticatory margin less reduced than in female castes, and without large gaps between them; ventral mandibular process lacking.

Trunk (Fig. 7) similar to that of queen, but somewhat longer; mesonotum with an impressed Mayrian furrow; scutellum higher; propodeum lacking spines, pinched laterally below spiracles, and extending out posteriorly beyond back margin of scutellum. Postpetiole with node very low and rounded; postpetiole low, smooth, and more elongate than in females; legs long and slender. Parameres curving sharply ventrad midway along length, with narrow, rounded tips having very short pilosity. Digitus heavily sclerotized, curving strongly ventrad near base, and rounded distally; cuspidal lobes very low and inconspicuous. Aedeagus subrectangular, ventral margin serrate, with tiny, very sharp recurved teeth. Wings as in *Pristomyrmex*, but with a complete discoidal cell (m-cu vein present).

Male known only for *A. ferox*; for further details see description of that species.

Larva. Known for two species. The larvae of *A. ferox* are considerably different from those of *A. notabilis* (see Wheeler and Wheeler, 1977, 1983, and in preparation). The differences are strong enough to suggest separation at the generic or even tribal level (Wheeler and Wheeler, personal communication). The alternative is a rapid evolution of the larvae within the genus *Acanthomyrmex* (see section on relationships).

SYNONYMIC LIST OF SPECIES

luciolae group.

- basispinosus* sp. nov. Sulawesi.
crassispina Wheeler, 1930. Taiwan.
dusun Wheeler, 1919. Sarawak.
ferox Emery, 1893. Peninsular Malaysia, Borneo, Sumatra.

laevis sp. nov. Peninsular Malaysia.
luciolae Emery, 1893. Sri Lanka.

notabilis group.

- careoscrobis* sp. nov. Sarawak.
concaus sp. nov. Sarawak.
foveolatus sp. nov. Sarawak.
mindanao sp. nov. Philippines, Sarawak.
notabilis (Smith), 1860. Moluccas, Sulawesi, Seram.

Misplaced *Acanthomyrmex*

Acanthomyrmex kochi Emery, 1909: 252, fig. 1. Minor worker from Etna Bay, New Guinea. The complete promesonotal suture, deeply impressed metanotal groove, finely punctate cephalic sculpture and other characters are at variance with all other material ascribed to *Acanthomyrmex* (Emery, 1922). This appears to be a *Pheidole* (*Pheidolacanthinus*).

KEY TO ACANTHOMYRMEX MINOR WORKERS

The minor workers of *A. dusun* and *foveolatus* are unknown.

1. Head convex across posterior margin, with at most a feeble medial concavity in full-face view (Fig. 57) 2
- Head distinctly concave across posterior margin 4
- 2(1). Petiole without long, cylindrical spines laterally on apex of node (Fig. 62) *notabilis*
- Such spines are present (Fig. 8D–F) 3
- 3(2). Head with conspicuous alveolate sculpture *ferox*
- Head virtually free of sculpture, smooth *laevis*
- 4(1). Head deeply concave across posterior margin (Figs. 9, 44) 5
- Head feebly concave across posterior margin in full face view (e.g., Fig. 15) 7
- 5(4). Propodeal spines in profile with a wide basal portion abruptly narrowing to shaft of spine (Fig. 10) *basispinosus*
- Propodeal spines lack a distinct wide base 6
- 6(5). Gaster with numerous long erect to suberect hairs; from Sri Lanka *luciolae*
- Gaster virtually bare; from Sarawak *concaus*
- 7(4). Propodeal spines somewhat laterally compressed, appearing blade-like in lateral view (Fig. 16); from Taiwan (Lanyu Island) *crassispina*
- Propodeal spines, cylindrical, not at all blade-like 8
- 8(7). Well-developed small projecting lobes immediately on each side of medial hair

- on anterior margin of clypeus; funicular scrobes present *mindanao*
- Medial clypeal lobes poorly developed; scrobes for scapes present, but these not bent down posteriorly to form funicular scrobes above eyes *careoscrobis*

KEY TO ACANTHOMYRMEX MAJOR WORKERS

The major workers of *A. careoscrobis*, *concaus*, and *laetis* are unknown.

1. Posterior margin of head conspicuously bilobed when head viewed in full-face (*luciolae* group, e.g., Fig. 11) 2
- Posterior margin of head not strongly bilobed, at most slightly emarginate mesad (*notabilis* group, e.g., Fig. 48, 59) 6
- 2(1). Propodeal spines somewhat laterally compressed, appearing blade-like in lateral view (Fig. 18); from Taiwan (Lanyu Island) *crassispina*
- Propodeal spines, cylindrical, not at all blade-like 3
- 3(2). Propodeal spines in profile with a wide basal portion abruptly narrowing to shaft of spine (Fig. 12) *basispinosus*
- Propodeal spines lack a distinct wide base 4
- 4(3). Node of petiole with long lateral spines at apex (Fig. 8D-F)² *ferox*
- Without long spines on petiole 5
- 5(4). Head costate across frons; from Sri Lanka *luciolae*
- Head lacking costae; from Borneo *dusun*
- 6(1). Postpetiole wide, less than 60% as long as it is wide in dorsal view *notabilis*
- Postpetiole about as wide as it is long in dorsal view 7
- 7(6). Dorsum of head with tiny, shallow foveae except for large foveae bordering antennal scrobes (Fig. 48) *foveolatus*
- Foveae larger (Fig. 53) *mindanao*

THE LUCIOLOE GROUP

Posterior margin of head in major workers emarginate, so that the back of the head is distinctly bilobed in full face view. Other characters: propodeal spiracle opening in majors larger and more conspicuous than in *notabilis* group majors; basal funicular segments in both castes

tending to be relatively slender (width of the second and third funicular segments less than 25% greater than their average length in minor workers, and less than 50% in majors); hypostomal teeth invariably present in majors. Except in *A. crassispina*, dorsal surface of gaster with numerous scattered hairs.

Species in this group are known from Sri Lanka, Peninsular Malaysia, the Malay Archipelago, and Taiwan.

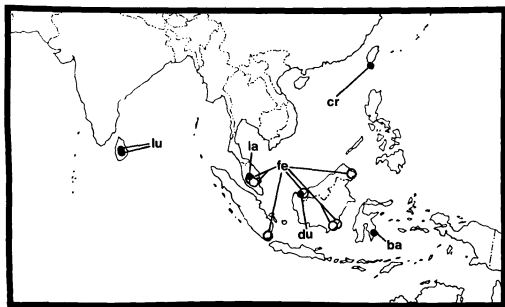
Acanthomyrmex basispinosus new species Figures 8A, 9-14; Map 1

Holotype. Minor worker deposited in MCZ from Indonesia: S.E. Sulawesi: 1-2 km east of Wolasi, 42 km south of Kendari, ca. 350 m, rotten wood in rainforest, W-46, 13-14 July 1972 (W. L. Brown, Jr. [examined]). Name derived from Latin *basis* + *spina*, referring to the widened bases of the propodeal spines.

Diagnosis. Propodeal spines of both castes with distinctive widened bases (Figs. 10, 12; postpetiole narrow, much wider than long in dorsal view).

Minor. Holotype (HW 1.08) and five minor worker paratypes measure HW 0.98 to 1.13, HL 0.95 to 1.08 (CI 103 to 105), ML 0.18 to 0.19 (MI 72 to 77), SL 1.06 to 1.20 (SI 97 to 115), EL 0.21 to 0.23, HFL 1.28 to 1.39 (FLI 124 to 136; FWI 16 to 17) mm. Head strongly concave across posterior margin in full-face view, and thus similar in shape to *A. luciolae* and *concaus*, except less broad (CI < 120), and lateral margins relatively more convex; widest above eyes. Head with rounded, thick-walled foveae (although foveae near scrobe, on side of head and on vertex with thinner walls, and thus approach the condition described for *A. ferox*). Dorsum of head with longest hairs extending about 0.18 mm. As in *A. notabilis*, short but conspicuous wide sulcus present mesad between the eyes above the frontal area (traces of such a sulcus present in some *A. luciolae*, *crassispina* and *concaus* specimens). Clypeal index 102 to 110. Lobe to each side of medial clypeal hair moderately to strongly produced; lateral clypeal

² Presumably the major of *A. laetis* will also key out here.



Map 1. Distribution of the species in the *luciolae* species group.

Abbreviations: ba = *A. basispinosus*, cr = *A. crassispinosa*, du = *A. dusun*, fe = *A. ferox*, la = *A. laevis*, lu = *A. luciolae*.

hairs in a completely enclosed fovea. Rugum extending back across clypeus from each of these medial clypeal lobes present, though poorly developed. Mandibles lacking a ventral tooth.

Spines on trunk virtually straight. Propodeal spines somewhat longer than those on pronotum; in the two largest specimens (HW for both 1.13 mm) propodeal spines considerably longer, as pronotal spines are very short and stubby. Propodeal spines with a distinctive widened base in profile.

Pronotal spines without conspicuous hairs. Pronotal angle abrupt but not forming a feeble tooth. Propodeal declivity bordered on each side by two adjacent rugae, which extend down from base of each propodeal spine (second rugum feeble).

Node of petiole as in Figure 8A, without sharp lateral denticles; PW1 intermediate (79 to 84). Anterior peduncle of petiole long and narrow, with the lateral hairs present and sublateral hairs lacking; subpetiolar declivity absent. Postpetiole nar-

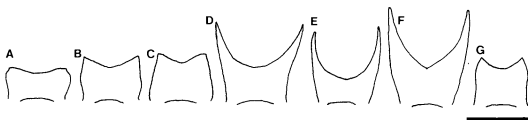


Figure 8. Petiolar nodes of minor workers in posterior view: *luciolae* species group. A. *A. basispinosus* paratype; B. *A. crassispina* syntype; C. *A. dusun* holotype (major worker); D. *A. ferox* syntype; E. *A. ferox* (*A. dyak* syntype); F. *A. laevis* paratype; G. *A. luciolae* syntype.

Scale line. 0.25 mm.

row, almost twice as wide as it is long in dorsal view, and with a high, narrow node; thus the postpetiole resembles that of *A. notabilis*. Femora with scattered hairs, and conspicuously concave beneath; hind femora relatively slender (FWI < 18). Color orange yellow or reddish yellow, legs lighter yellow.

Major. The two paratypes measure HW 2.10 to 2.18, HL 2.17 to 2.24 (CI 97), SL 1.18 (SI 54 to 56), EL 0.28, HFL 1.40 to 1.44 (FLI 64; FWI 16) mm. Foveae on head denser, more deeply impressed, and somewhat larger than in *A. crassispina* and *dusun*. Without a distinct cephalic hollow. Long feeble darkly pigmented medial streak dorsad on head; wide medial sulcus conspicuous on frons. Clypeal index larger than in minors: 126 and 139. Forward margin of clypeus lacking a medial projection (but with two feeble, rounded lobes medially). Propodeal spines as described for minor worker.

Paratypes. Two majors and five minors, same date and collection number as holotype (MCZ, BMNH).

Additional Records. Known only from type series.

Acanthomyrmex crassispina

Figures 8B, 15–20; Map 1

Acanthomyrmex crassispina Wheeler, 1930: 101–103, fig. 2. Taiwan: Botel Tobago (=Lanyu Island), 6/1926, no. 49, three minor workers (R. Takahashi, MCZ and U.S. National Museum [examined]).

Diagnosis. Both castes with each scape having a small lateral flange proximad; propodeal spines wide and blade-like in profile; pilosity very sparse; from Taiwan.

Minor. Syntypes measuring HW 1.07 to 1.09, HL 0.87 to 0.90 (CI 121 to 123), ML 0.75 to 0.78 (MI 86 to 89), SL 0.97 to 0.98 (SI 90 to 91), EL 0.16 to 0.17, HFL 1.08 to 1.10 (FLI 122 to 125; FWI 23 to 24) mm. Head concave across posterior margin in full-face view, although not as strongly as in *luciolae*. Head widest above eyes. Head with rounded, thick-walled foveae, and dorsally with very few, scat-

tered hairs (these standing 0.08 to 0.10 mm). Scares virtually smooth, not feebly rugose as in most *Acanthomyrmex*. Scares also with a distinctive lateral flange extending longitudinally at their bases (Fig. 15). Clypeal index 128–131. Lobe to each side of medial clypeal hair very feeble, and relatively widely separated from the hair; lateral clypeal hairs not in a completely enclosed fovea. A well-developed rugum extends back from each of the medial clypeal lobes, separating a smooth medial clypeal region from the more lateral areas. Mandibles lacking a ventral tooth.

Spines on trunk slightly curved caudad; propodeal spines somewhat longer than those on pronotum, and also slightly compressed laterally so as to appear wide and blade-like in profile. Pronotal spines lacking conspicuous hairs. Pronotal angle not forming a feeble tooth. Sculpture on trunk (particularly on dorsum) relatively feebly impressed. Propodeal declivity bordered on each side by a single rugum extending from the base of each propodeal spine.

Node of petiole as in Figure 8B, PWI intermediate (88 to 92); node lacking the single pair of hairs found low on caudal face of petiolar node of other *Acanthomyrmex* species. Anterior peduncle of petiole relatively short and deep, lacking lateral and sublateral hairs; subpetiolar declivity present. Postpetiole subrectangular, almost as long as it is wide in dorsal view, and with two or three conspicuous rugae on each side; lacking pilosity. Gaster virtually without pilosity. Femora lacking all but basal hairs, and with ventral surfaces flattened or only very feebly concave. Head and trunk orange yellow, with legs yellow.

Major. Individual from Botel Tobago (Lanyu Island, Taiwan) measures HW 1.99, HL 2.11 (CI 94), SL 1.03 (SI 52), EL 0.25, HFL 1.32 (FLI 62; FWI 19) mm. As in the minor, head, trunk, and gaster with very little long pilosity. Head as wide below eyes near mandible bases as above eyes (greatest HW is above eyes in other

species). Shallow oval foveae scattered over head surface, not as dense as in other *luciolae* group species; foveae most numerous laterally and on vertex. Cephalic hollow well-developed, with medial sulcus extending below it to the frontal area shallow and inconspicuous. Darkly pigmented medial streak very short, present between lobes on vertex but not extending to cephalic hollow. Forward margin of clypeus lacking a medial projection, although two low, rounded lobes are present. Propodeal spines moderately long, curved caudad; compressed as in the minor worker. Scape with lateral flange near base. PWI value 100.

Additional Records. TAIWAN: Botel Tobago (=Lanyu Island), three minor workers and one major (T. Kano, MCZ, BMNH). This series lighter yellow in color (except gaster dark brownish yellow); femora convex ventrad.

Acanthomyrmex dusun
Figures 8C, 21–22; Map 1

Acanthomyrmex dusun, Wheeler, 1919: 89. Malaysia: W. Sarawak: Mount Matang, i/1914 (G. E. Bryant, MCZ [examined]).

Diagnosis. Major with head lacking rugae; clypeus with medial projection; propodeal spines short, cylindrical, curved ventrad. Minor worker unknown.

Major. HW 2.00, HL 1.99 (CI 100), SL 0.95 (SI 48), EL 0.21, HFL 1.08 (FLI 54; FWI 21) mm. Shallow oval foveae scattered, somewhat larger and denser near scrobes; traces of longitudinal rugae near scrobes. With a more clearly demarcated funicular scrobe than in any other *Acanthomyrmex* major examined. Cephalic hollow well-developed, with a conspicuous medial sulcus extending below it to the frontal area. Darkly pigmented medial streak on head long, extending into

hollow. Clypeal index 178. Forward margin of clypeus with a medial projection. Condition of hypostomal teeth unknown.

Propodeal spines short, conspicuously curved caudad. Pronotal angle drawn out into a feeble tooth. Node of petiole as in Figure 8C, PWI intermediate (ca. 69). Anterior peduncle of petiole relatively short and deep, and with lateral hairs present, but sublateral pair lacking; subpetiolar declivity present. Postpetiole subrectangular, similar to that of *A. crassispina*. Dorsal surface of postpetiole and gaster hairy. Femora hairy, and with ventral surfaces distinctly concave. Color orange yellow.

Additional Records. Known only from holotype.

Acanthomyrmex ferox
Figures 3–7, 8D–E, 23–28; Map 1

Acanthomyrmex ferox Emery, 1893: 245–246, pl. 6, fig. 11. Peninsular Malaysia: Perak, two minor workers (M. M. Staudinger, MCSN and MHN [examined]).

Acanthomyrmex dyak Wheeler, 1919: 86–89. Malaysia: Sarawak: Kuching, two minor workers and one major (J. Hewitt, MCZ [examined]). NEW SYNONYMY.

Diagnosis. Petiolar node of both worker castes with long, dorsally directed lateral spines, and postpetiole with a high, rounded node. Minor worker with conspicuous alveolate sculpture.

Minor. The two syntypes measure HW 1.06 to 1.12, HL 1.00 to 1.05 (CI 106 to 107), ML 0.83 (MI 83), SL 1.26 to 1.28 (SI 114 to 120), EL 0.20 to 0.21, HFL 1.38 to 1.39 (FLI 132 to 139; FWI 19 to 20) mm. Head shape as in *A. notabilis*, i.e., virtually rounded across posterior margin in full-face view, although slightly flattened or with a trace of a concavity mesad. Maximum head width virtually the same above and below eyes. Cephalic sculpture

Figures 9–14. *Acanthomyrmex basispinosus* paratypes. 9. Frontal view of head, minor worker. 10. Lateral view of trunk, minor worker (insert: lateral view of individual with short pronotal spines). 11. Frontal view of head, major worker. 12. Lateral view of trunk, major worker. 13. Dorsal view of postpetiole, minor worker. 14. Lateral view of waist, minor worker.

Scale lines. Figures 9–12, 0.50 mm. Figures 13–14, 0.10 mm.

best described as areolate or alveolate rather than foveate, as the foveae have angular walls and are separated by thin partitions; longer hairs on dorsum of head extend 0.15 mm. Clypeal index 91 to 93. Feeble lobe present on each side of medial clypeal hair; lateral clypeal hairs not in a well-defined fovea. Clypeus virtually smooth, and without two longitudinal rugae present to demarcate a medial clypeal region. Mandibles lacking a ventral tooth.

Spines on trunk virtually straight (propodeal spines with a slight curvature caudad); pronotal spines hairy, and consistently longer than those on propodeum. Pronotal angle drawn out into a feeble tooth (Fig. 24: indistinct or absent in some other specimens and on one side of a syntype). Propodeal declivity bordered on each side by a single rugum, as described for *A. crassispina*.

Node of petiole as in Figure 8D-E, PWI wide (120 and 138). Anterior peduncle of petiole relatively short and deep, and with lateral and sublateral hairs; subpetiolar declivity present. Postpetiole smooth (although with feeble foveae on node); with convex lateral margins in dorsal view (rather than rectangular), and almost as long as it is wide. Postpetiole having a distinctive high, rounded node with scattered hairs. Dorsal surface of gaster hairy, but with hair density sparser than in most other *luciolae* group species. Femora hairy, and with ventral surfaces only feebly concave. Orange yellow, with legs and gaster lighter and with more yellow.

Major. Three Sarawak majors from two series (single major from Peninsular Malaysia very similar): HW 2.42 to 2.58, HL 2.45 to 2.48 (CI 99 to 104), SL 1.20 to 1.25 (SI 47 to 52), EL 0.26 to 0.28, HFL 1.54 to 1.56 (FLI 63 to 68; FWI 20) mm. Frons costate up to level of scrobes (and laterally

up to level of eyes); vertex relatively densely foveate (comparison of specimens suggests the foveae become denser and more deeply impressed in progressively smaller majors; note that the major in Fig. 25 is relatively large). No distinct cephalic hollow. No darkly pigmented streak dorsad on head; wide medial sulcus conspicuous, low on face. Forward margin of clypeus with a medial projection. Propodeal spines long, as in minors but thicker at bases. Pronotal angle lacking the feeble tooth characteristic of the minor caste.

Queen. Previously underscribed. Three queens (from Peninsular Malaysia, Sarawak, and Kalimantan) measure HW 1.86 to 2.30, HL 1.54 to 1.83 (CI 121 to 126), ML 1.08 to 1.20 (MI 65 to 70), SL 1.10 to 1.21 (SI 52 to 59), EL 0.28 to 0.33, HFL 1.53 to 1.68 (FLI 92 to 97; FWI 20 to 21) mm. Head (Fig. 4) broad, with lateral margins divergent, and widest near vertex; posterior margin slightly concave mesad. Head with narrow, wavy longitudinal rugae, forming foveae behind level of ocelli and laterally; foveae feeble beneath head. Medial sulcus narrow but conspicuous beneath ocelli. Scrobes prominent, as in majors. Clypeus smooth, with projecting medial lobe as in major. Trunk (Fig. 5) irregularly rugose laterally (especially on propodeum), smoothest on anepisternum and pronotum. Dorsum with numerous foveae, and with rugae extending forward onto mesonotum from its posterior border. Posterior margin of scutellum with short, stout horns laterally. Propodeal spines short and stout, projecting caudad. Anterior peduncle of petiole short and deep; node of petiole broad, with lateral spines greatly shortened relative to worker castes. Postpetiole narrower than in workers, more than 50% wider than long in dorsal view. Petiole and postpetiole with

Figures 15–20. *Acanthomyrmex crassispina* from Botel Tobago (Taiwan). 15. Frontal view of head, minor worker. 16. Lateral view of trunk, minor worker. 17. Frontal view of head, major worker. 18. Lateral view of trunk, major worker. 19. Oblique dorsal view of postpetiole, minor worker. 20. Lateral view of waist, minor worker.

Scale lines. Figures 15–18, 0.50 mm. Figures 19–20, 0.10 mm.

pocket on rock, 20/ix/1977, five minor workers and one major (B. Bolton, BMNH). *Sabah*: Gunung Silam, 440 m, no. A-12, 7 Jan. 1983, two minors and one major (R. Leakey, BMNH). *INDONESIA*: *S.E. Kalimantan (Borneo)*: Pleihari-Martapura Reserve, lowland rainforest, nesting in leaf litter, 5 July 1983, 47 minor workers, two majors, seven males, and one dealate queen (M. W. Moffett and D. A. Fletcher, MCZ, BMNH, MCSN and MHN); 17–46 km W. Batulitjin, lowland rainforest, under bark of rotten stump, 2 July 1972, one minor worker (W. L. Brown, Jr., MCZ). *Sumatra*: Lampongs, Pedada-B. 22/I/1922, two minor workers (MCZ and BMNH).

Height of pilosity variable, with the longer hairs dorsally on the head extending about 0.15 mm in the syntypes and in the specimens from Kalimantan, Pahang (Malaysia) and the Gombak (Malaysia) specimen collected by Imai, but shorter (0.08 to 0.10 mm) in other series. Most of the workers with shorter cephalic pilosity have relatively sparse (and very short) pilosity on their gasters, and some also lack pilosity on their pronotal spines.

The traces of very fine rugulose sculpture present on the lateral surfaces of the mandibles of most *Acanthomyrmex* minor workers is generally absent in *A. ferox*, although this microsculpture can be discerned in the types. Petiolar node with spine length and curvature somewhat variable (Fig. 8D–E), PWI 105 to 143. Postpetiole of all major workers and some minors (i.e., those from Lampongs and Sarawak) with conspicuous foveae on node, as in individual in Figure 27. Femora sometimes more concave beneath than in syntypes, particularly in the Bolton specimens from Sarawak and the Perak (Malaysia) worker. Color in most specimens darker than in syntypes, reddish orange.

A. dyak minor syntypes (HW 1.00 and 1.04 mm) very similar to other *A. ferox* material; major syntype small (HW 2.28 mm), but not as small as the Sabah major (HW 1.98 mm); otherwise very similar to the Sarawak specimens described above.

Tooth lacking at pronotal angle in both castes. Femora flattened or at most feebly concave beneath.

Natural History. A colony of nearly fifty workers was collected in southern Borneo nesting in leaf litter in disturbed primary rainforest (see Moffett, 1985).

Acanthomyrmex laevis new species Figures 8F, 29–32; Map 1

Holotype. Minor worker deposited in MCZ from Peninsular Malaysia: Perak: Ringlet Pass, 28 Feb. 1982 (M. Kubota). Name refers to lack of sculpture on head.

Diagnosis. Very similar to *A. ferox*, but head of minor worker smooth, lacking all but traces of sculpture. Major worker unknown.

Minor. Holotype measures HW 1.03, HL 0.96 (CI 107), ML 0.80 (MI 83), SL 1.29 (SI 126), EL 0.21, HFL 1.42 (FLI 148; FWI 18) mm. Very similar in all respects to *A. ferox*, except head lacking sculpture dorsally and with only traces of rugae laterally and beneath head. The head sculpture is strongly developed in all *A. ferox* specimens, including one from the same locality as the *A. laevis* holotype.

In addition, the petiolar node of *A. laevis* (Fig. 8F) has somewhat longer petiolar spines than in *A. ferox* specimens, and the crotch between the spines is relatively narrow basally (in *ferox*, the crotch has a wide, convex base). A well-defined subpetiolar declivity is lacking, although a feeble declivity occurs. Node of postpetiole smooth (as in some *A. ferox*). Pronotal angle not forming a feeble tooth. Uniform dark orange red.

Additional Records. Known only from holotype.

Acanthomyrmex lucirolae Figures 8G, 33–38; Map 1

Acanthomyrmex lucirolae Emery, 1893: 245–246, pl. 6, fig. 5–10. Sri Lanka: Kandy, two minor workers and one major (E. Simon, MCSN and MHN [examined]).

Diagnosis. Minor workers with posterior margin of head deeply concave; head

oped ruga extends back from each of these medial clypeal lobes, as described for *A. crassispina*. Mandibles lacking a ventral tooth.

Spines on trunk exceptionally long; pronotal spines straight and propodeal spines somewhat longer, slender and elegantly curved (Fig. 34). Pronotal spines with one to three conspicuous hairs. Pronotal angle not forming a feeble tooth. Propodeal declivity bordered on each side by two adjacent rugae, as described for *A. basispinosus*.

Petiole as in Figure 8G, PWI intermediate (67 to 70). Anterior peduncle of petiole long and narrow, with lateral hairs present, but sublateral hairs lacking; subpetiolar declivity present. Postpetiole much as described for *A. crassispina*, except hairier, and dorsum raised into a low node anteriorly, rather than evenly rounded in profile. Femora hairy, and with ventral surfaces only feebly concave. Color light orange yellow, legs yellow.

Major. Syntype measures HW 1.80, HL 1.83 (CI 98), SL 1.03 (SI 57), EL 0.26, HFL 1.26 (FLI 69; FWI 22) mm. Head sculpture as described for *A. ferox*, but costate sculpture on frons extending relatively farther back towards vertex, and foveae relatively feebler on sides of head. Without a distinct cephalic hollow. No darkly pigmented medial streak dorsad on head; wide medial sulcus conspicuous, low on face. Forward margin of clypeus without a medial projection. However, two feeble lobes are present, each with a single notch along their margins. Propodeal spine relatively short and virtually straight, in contrast to condition in the minor worker. Subpetiolar declivity lacking (although present in minor caste). Head and gaster a deeper orange than in minors.

Additional Records. SRI LANKA: Kandy, 600–700 m, nos. 1236 and 1240, VII/

10–13/1955, two minor workers (E. O. Wilson, MCZ); Gilimale, 16–20 km NE of Ratnapura, nos. 1292, 1310, 1325, and 1354, VII/18–21/1955, six minor workers (E. O. Wilson, MCZ, BMNH). Several of the Wilson specimens have longer (up to 0.25 mm) pilosity on the head and relatively hairy pronotal spines; also some specimens lack the tibial spur usually present on the middle and hind legs of *Acanthomyrmex* ants. PWI 57 to 76. Most of these ants are darker and more red than syntypes.

THE NOTABILIS GROUP

Dorsal margin of the head of the majors at most very slightly notched mesad so that in full-face view margin appears rounded or somewhat flattened, but not strongly bilobed. Other characters: majors with propodeal spiracle opening slightly smaller and less conspicuous than in *luciolae* group; basal funicular segments relatively thick (width of the second and third funicular segments more than 25% greater than their average length in minor workers and less than 50% in majors), except in *A. notabilis*; hypostomal teeth often absent in majors. Dorsal surface of gaster invariably with very few (if any) long hairs.

All species in this group are from the Malay Archipelago; as yet none have been collected from the Asian mainland.

Acanthomyrmex careoscrobis new species Figures 39A, 40–43; Map 2

Holotype. Minor worker deposited in BMNH from Malaysia: Sarawak: 4th Div., Gunung Mulu National Park, mixed dipterocarp forest, 200 m, pit-fall trap, 14/III/1978 (N. M. Collins). Name derived from Latin *careo* + *scrobis*, referring to the lack of scrobes for retracted funiculi.

Diagnosis. Similar to *A. mindanao*, but lacking even a poorly developed funicular

Figures 33–38. *Acanthomyrmex luciolae* from Kandy. 33. Frontal view of head, minor worker. 34. Lateral view of trunk, minor worker. 35. Frontal view of head, major worker. 36. Lateral view of trunk, major worker. 37. Dorsal view of postpetiole, minor worker. 38. Lateral view of waist, minor worker.

Scale lines. Figures 33–36, 0.50 mm. Figures 37–38, 0.10 mm.



Map 2. Distribution of the species in the *notabilis* species group.

Abbreviations: ca = *A. careoscrabis*, co = *A. concavus*, fo = *A. foveolatus*, mi = *A. mindanao*, no = *A. notabilis*.

scrobe; without strongly projecting medial clypeal lobes. Major worker unknown.

Minor. Holotype measures HW 0.94, HL 0.79 (CI 118), ML 0.70 (MI 88), SL 0.80 (SI 86), EL 0.16, HFL 0.83 (FLI 105; FWI 24) mm. Head shape similar to *A. mindanao*, but slightly more deeply concave across posterior margin. Maximum head width virtually the same above and below the level of the eyes. Head with rounded foveae having thick walls; dorsally the longest hairs extend about 0.10 mm. Without any trace of grooves to retain retracted funiculi adjacent to scrobes for each scape. Scapes relatively short, barely overreaching back margin of head when retracted to scrobes. Clypeal index

178. Lobe to each side of medial clypeal hair feeble (essentially absent) and widely separated from the hair; lateral clypeal hairs apparently not in a completely enclosed fovea, but sculpture difficult to interpret. Smooth medial area of clypeus bordered by longitudinal rugae laterally. Mandibles lacking a ventral tooth.

Spines on trunk relatively longer than in *A. mindanao*, with pronotal spines in particular not as reduced in length. Pronotal spines with one hair or none. Pronotal angle not forming a feeble tooth. Propodeal declivity bordered on each side by a single rugum.

Node of petiole as in Figure 39A, PWI narrow (ca. 49). Anterior peduncle of petiole shorter and deeper than in *A. mindanao* and other species in the genus, and with lateral petiolar hairs present and sub-lateral hairs lacking; subpetiolar declivity present. Postpetiole (Fig. 42) similar to *A. mindanao*; with two pairs of hairs dorsally and two lateral pairs. Femora with scattered hairs throughout length, and with ventral surfaces distinctly concave; hind femora relatively short (FLI < 110). Orange yellow, with legs yellow.

Additional Records. Known only from holotype.

Acanthomyrmex concavus new species Figures 39B–C, 44–47; Map 1

Holotype. Minor worker deposited in BMNH from Malaysia; Sarawak; 4th Div., Gunung Mulu National Park, RGS Exped., Long Pala, lowland rainforest leaf litter, 19/X/1977 (B. Bolton). Name refers to strongly concave posterior margin of head.

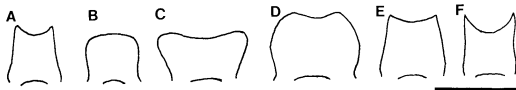


Figure 39. Petiolar nodes of minor workers in posterior view: *notabilis* species group. A. *A. careoscrabis* holotype; B. *A. concavus* holotype; C. *A. concavus* from Sabah; D. *A. foveolatus* holotype (major worker); E. *A. mindanao* paratype; F. *A. notabilis* from Sulawesi.

Scale line. 0.25 mm.

hair; lateral clypeal hairs in a completely enclosed fovea. Smooth medial area of clypeus not bordered laterally by rugae. Mandibles with a small but distinct ventral tooth.

Spines on trunk virtually straight, with propodeal spines extending more directly caudad than in other species; pronotal spines short, stubby, and lacking conspicuous hairs. Pronotal angle forming a feeble tooth. Sculpture on trunk particularly deeply impressed. Propodeal declivity transversely rugose, and bordered on each side by two adjacent rugae.

Petiolar node rounded, without dorso-lateral teeth (Fig. 39B), so that PWI not measurable. Anterior peduncle of petiole long and narrow, and lacking lateral and sublateral hairs; subpetiolar declivity present. Postpetiole subrectangular, about one third wider than it is long, rounded dorsad and only feebly rugose on sides; with two pairs of hairs dorsally. Femora hairy, and with ventral surfaces distinctly concave; hind femora relatively short (FLI < 120). Color dark orange red, with legs and gaster lighter and more orange.

Paratypes. One minor worker, same collection data as holotype (MCZ).

Additional Records. MALAYSIA: *Sarawak*: 4th Div., Gunung Mulu National Park, camp 5, B.M. 1978-49, v-viii/1978, one minor worker (P. M. Hammond and J. E. Marshall, BMNH). *Sabah*: Gunung Silam, 330 m, no. A-6, 9/2/1983, one minor worker (R. Leakey, BMNH). The *Sabah* specimen has a distinctive, bilobed petiolar node (Fig. 39C).

***Acanthomyrmex foveolatus* new species**
Figures 39D, 48-50; Map 2

Holotype. Major worker deposited in MCZ from Malaysia: Sarawak: Mount Poi, 200 ft. (E. Mjöberg). Name referring to cephalic sculpture.

Diagnosis. Major worker similar to that of *A. mindanao*, but with foveae on head very tiny and numerous. Minor worker unknown.

Major. Holotype measures HW 2.22, HL 2.49 (CI 90), SL 0.97 (SI 44), EL 0.22,

HFL 1.16 (FLI 47; FWI 19) mm. Foveae on head numerous (even in vicinity of clypeus), very tiny and shallow (except for larger foveae along borders of antennal scrobes and beneath head, where foveae become confluent). Head virtually lacking pilosity. Cephalic hollow present but not as conspicuous as in *A. mindanao*. A darkly pigmented streak extends to hollow from dorsum of head; wide medial sulcus conspicuous from hollow to frontal area. Clypeal index 174. Forward margin of clypeus lacking a medial projection. Hypostomal teeth present.

Propodeal spines short, with distinctly thickened bases; bent caudad. Pronotal angle drawn out into a distinct tooth. Node of petiole without distinct dorsolateral denticles or spines (Fig. 39D), PWI narrow to intermediate (ca. 64). Anterior peduncle of petiole long and narrow, and lacking both lateral and sublateral petiolar hairs; subpetiolar declivity lacking. Postpetiole subrectangular, similar to that of *A. mindanao*; with only two pairs of hairs dorsally. Femora with scattered hairs, and with ventral surfaces distinctly concave. Orange yellow, with legs yellowish orange; head a richer orange and with contrasting yellow antennae.

Additional Records. Known only from holotype.

***Acanthomyrmex mindanao* new species**
Figures 39E, 51-56; Map 2

Holotype. Minor worker deposited in MCZ from Philippines: Mindanao: Davao Province, east slope of Mount McKinley, 3,300 ft., lot 33, under bark, 30 August 1946 (F. C. Werner). The specific name is a noun in apposition after the type locality.

Diagnosis. Postpetiole in both castes approximately cuboidal, not conspicuously wider than deep in dorsal view; propodeal spines shorter than in *A. notabilis*. Minors with posterior margin of head moderately concave in dorsal view, and with funicular scrobe present, although poorly developed; ventral mandible tooth usually present, and with strongly projecting medial clypeal lobes.

species; lateral clypeal hairs not in a completely enclosed fovea. Smooth medial area of clypeus not bordered laterally by distinct rugae. Mandibles with a tiny but distinct ventral tooth.

Spines on trunk short relative to other species, propodeal spines conspicuously longer than pronotal spines, and are virtually straight to feebly curved caudad; pronotal spines very short and stubby (lacking in larger minor workers in some other series: see below). Pronotal spines without conspicuous hairs. Pronotal angle never drawn out into a feeble tooth. Propodeal declivity bordered on each side by one rugum or possibly two adjacent rugae (second rugum poorly developed when present).

Node of petiole as in Figure 39E, PWI narrow (45 to 64); caudal face of node usually with a pair of hairs near summit (absent in Fig. 56), in addition to the single pair found lower on the same face of node in this and most other *Acanthomyrmex*. Anterior peduncle of petiole relatively short and deep as in *A. notabilis*, and with lateral petiolar hairs present (but sometimes hair missing from one side of petiole); sublateral pair lacking. Subpetiolar declivity present. Postpetiole subrectangular, almost as long as it is wide in dorsal view, and with two or three longitudinal rugae on each side; hairy dorsally. Femora only with basal hairs or having one to three additional hairs, and with ventral surfaces distinctly concave; hind femora relatively short ($FLI < 110$). Orange yellow to reddish orange, with legs lighter yellow.

Major. Paratype measures HW 1.98, HL 2.16 (CI 92), SL 0.90 (SI 46), EL 0.26, HFL 1.00 (FLI 46; FWI 20) mm. Foveae on head smaller and shallower than in *A. notabilis* (somewhat larger and denser beneath head), numerous except very few present in area between antennal scrobes. Pilosity present on head, but more scattered than in *A. notabilis* majors. Cephalic hollow conspicuous. A darkly pigment-

ed streak extends to hollow from dorsum of head; wide medial sulcus conspicuous from hollow to frontal area. Forward margin of clypeus with a medial projection. Hypostomal teeth absent. Propodeal spines short and curved caudad. Color as in minor workers, but head a richer orange, antennae a contrasting shade of yellow.

Paratypes. Four minor workers and one major, same locality data as holotype.

Additional Records. PHILIPPINES: *Mindanao*: Lanao District: Momungan, 6/20/1951, ten minor workers and one major (D. Empeso, MCZ and BMNH); Momungan, ser. B, 6/20/1951, thirteen minor workers (D. Empeso, MCZ); Olanog, 6/25/1951, eight minor workers (D. Empeso, MCZ, MCSN and MHN); Iligan, 1951, 29 minor workers (D. Empeso, MCZ); Ginoog, Misamis, Anakan Lbr. Co., 4/3/1935, nine minor workers (A. Reyes, MCZ). MALAYSIA: *Sarawak*: 4th Div., Gunung Mulu National Park, RGS Exped., Long Pala, lowland rainforest litter sample, 18.x.1977, three minor workers (B. Bolton, BMNH). The Philippine ants are very similar to the type series, except that the Momungan major is smaller (HW 1.64) and hairier than the paratype major. This major also has hypostomal teeth, and lacks a subpetiolar declivity. The Ginoog workers consistently lack the pair of hairs near the summit of the petiolar node which are usually present in specimens from other series. Color in a few specimens uniform yellow.

Workers of the Sarawak series are the smallest recorded for this genus (HW 0.70 to 0.76 mm), and are significantly smaller than any of the Philippine specimens (HW 0.90 to 1.11 mm). These ants lack a ventral mandibular tooth, lack sublateral hairs on their petioles, and have the pilosity on their postpetioles reduced to two pairs of hairs dorsally and one lateral pair.

The larger of the minor workers from the Philippines (HW > 1.05 mm) completely lack pronotal spines. Also, the same

individuals have better developed ventral mandibular teeth than in other minors; their gasters are somewhat hairier and they have a more deeply engraved frontal sulcus. They therefore show some characteristics intermediate between the minor and major castes.

Acanthomyrmex notabilis

Figures 39F, 57–62; Map 2

Pheidole notabilis F. Smith, 1860: 111, figs. 3–4. Indonesia: Moluccas: Batchian (i.e., Bacan Island), one minor worker and one major (A. R. Wallace, Hope Collection, University Museum, Oxford [examined]).

Acanthomyrmex notabilis—Emery, 1893: 244.

Diagnosis. Postpetiole of both worker castes narrow, much wider than deep in dorsal view; propodeal spines long; minors with head convex across posterior margin in dorsal view (except for very feeble medial concavity), without funicular scrobe, and with ventral mandible tooth lacking.

Minor. Syntype measures HW 1.01, HL 0.90 (CI 113), ML 0.73 (MI 82), SL 1.04 (SI 102), EL 0.17, HFL 1.13 (FLI 126; FWI 19) mm. Posterior margin of head convex in full-face view, although slightly flattened or with a trace of a concavity mesad. Maximum head width virtually the same above and below the level of the eyes. Head with rounded foveae having thick walls. As in *A. basispinosus*, short but conspicuous sulcus present mesad between the eyes above the frontal area. Dorsum of head with longest hairs extending about 0.12 mm. Scares long, conspicuously overreaching back margin of head when retracted to scrobes. Clypeal index 117 (114 to 128 in other minor worker material). Lobe to each side of medial clypeal hair feeble or moderately developed; lateral clypeal hairs in a completely enclosed fovea. Smooth medial area of clypeus not bordered laterally by distinct rugae. Mandibles lacking a ventral tooth (at least in specimens other than holotype, as the undersurface of the mandibles is not accessible in the latter).

Spines on trunk long, somewhat curved caudad (straighter in most specimens from other series); propodeal spines slightly longer than those on pronotum. Pronotal spines without conspicuous hairs. Pronotal angle forming a feeble but distinct tooth in most specimens, but not in holotype. Propodeal declivity bordered on each side by two adjacent rugae, as described for *A. basispinosus* (*luciolae* group).

Node of petiole as in Figure 39F, PWI narrow to intermediate (79 in syntype, and 47 to 89 in eight specimens from other series). Anterior peduncle of petiole relatively short and deep, and lacking both lateral and sublateral petiolar hairs; subpetiolar declivity absent. Postpetiole narrow (almost twice as wide as it is long in dorsal view) and with a relatively raised node, and resembling that of *A. basispinosus*, although with only two pairs of hairs dorsally. Femora lacking all but basal hairs; ventral surfaces distinctly concave, particularly in the hind legs. Reddish orange to orange yellow, legs lighter.

Major. Syntype measures HW 2.25, HL 2.30 (CI 98), SL 1.11 (SI 49), EL 0.25, HFL 1.23 (FLI 54; FWI 20) mm. Relatively large, shallow foveae on head widely scattered dorsally (virtually lacking in area immediately above clypeus), denser laterally. Cephalic hollow present but indistinct. A darkly pigmented streak extends to hollow from dorsum of head; wide medial sulcus conspicuous from hollow to frontal area. Clypeal index larger than in minors, 138 in holotype. Forward margin of clypeus lacking a medial projection (although two very feeble, rounded lobes are sometimes present). Hypostomal teeth not accessible to view in holotype; usually present in other material. Propodeal spines moderately long and almost straight (generally not quite as long and usually curving somewhat caudad in other *notabilis* material). Pronotal angle lacking the feeble tooth characteristic of the minor caste. Anterior node of petiole generally deeper than in minors.

Additional Records. INDONESIA: *Sulawesi*: SW slope of Mount Klabat, 400–600 m, rotten wood in rainforest, nos. B9-1, K-2, K-61, X-9, W1-7, and Y-22, 13–19/VI/1972, 24 minor workers and nine majors (W. L. Brown, Jr., MCZ and BMNH); Air Madidi slope of Mount Klabat, 400–600 m, rotten wood in wet forest, nos. H3-6 and L-8, 13–19/VI/1972, 13 minor workers and two majors (W. L. Brown, Jr., MCZ and BMNH); Tangkoko-Batuangus Reserve, 200 m, nesting in log in rainforest, 29 July 1983, 37 minor workers and three majors (M. W. Moffett and D. A. Fletcher, MCZ, BMNH, MCSN and MHN). *Seram*: above Haruru, near Masohi, 50–150 m, rotten wood in rainforest, no. M-122, 18 March 1981, 12 minor workers (W. L. Brown, Jr., MCZ and BMNH). *Seram* minor specimens tending to be somewhat smaller than those from Sulawesi (HW averaging [$\bar{X} \pm SE$] 1.13 ± 0.04 mm, versus 1.02 ± 0.04 mm for the Sulawesi minors; samples of 36 and 7 minors, respectively).

Natural History. The ants nest in cavities within logs in primary rainforests. Nests typically contain stores of fig seeds and other tiny seeds (see Moffett, 1985).

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